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The influence of disturbance events on pileated woodpeckers in Northeastern Oregon

Evelyn L. Bull [a,*], Nicole Nielsen-Pincus [b], Barbara C. Wales [a], Jane L. Hayes [a]

[a] USDA Forest Service, Pacific Northwest Research Station, 1401 Gekeler Lane, LaGrande, OR 97850, USA
[b] 4385 Happy Hollow Rd., Prineville, OR 97754, USA

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Abstract

The pileated woodpecker (*Dryocopus pileatus*) is a species of conservation concern and an indicator of mature and old forest habitat conditions in the Pacific Northwest. The effects of natural and human-caused disturbance on density of nesting pairs, reproductive success, and traditional home ranges were compared over 30 years in two areas and over 15 years in five additional areas. In one study area, density of nesting pairs of pileated woodpeckers decreased from five to one after extensive regeneration cuts eliminated most of the stands of mature and old-growth grand fir (*Abies grandis*) and reduced the density of nest and roost trees and foraging substrate since 1990. Density of nesting pairs, reproductive success, and home range location remained fairly consistent over 30 years in a second study area with extensive tree mortality resulting from insect outbreaks but without regeneration harvests. The amount of unharvested stands and closed canopy stands in home ranges were positively correlated with reproductive success, and the amount of area in harvested stands was negatively correlated with reproductive success in 2003–05. High tree mortality and subsequent loss of canopy closure in stands of grand fir and Douglas-fir from insect outbreaks did not appear to be detrimental to pileated woodpeckers provided that dead trees and logs were abundant and that stands were not harvested.
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Keywords: Disturbance; Harvest activity; Management; Northeast Oregon; Pileated woodpeckers; Reproduction

1. Introduction

The pileated woodpecker (*Dryocopus pileatus*) is considered a species of conservation concern and an indicator of mature and old forest habitat conditions in the Pacific Northwest. This large, primary cavity-nesting bird plays an important ecological role in older conifer forest ecosystems, feeding primarily on insects of downed and standing dead wood (snags). They excavate nest and roost cavities in large-diameter snags and live trees with decay that are eventually used by a wide variety of other birds and mammals (Bull and Jackson, 1995; Aubry and Raley, 2002a). Pileated woodpeckers are territorial and defend the entire territory or home range, particularly at the outer periphery, all year by calling and drumming on resonant wood. Availability of suitable habitat is probably a limiting factor for populations of pileated woodpeckers in northeastern Oregon (Bull and Holthausen, 1993).

Habitat for pileated woodpeckers has been described as late successional or mature coniferous or deciduous forests with dense canopy closure (Mellen et al., 1992; Bull and Holthausen, 1993; Renken and Wiggers, 1993; McClelland and McClelland, 1999; Aubry and Raley, 2002b). Several authors have described the positive association of pileated woodpeckers with the high densities of trees >30 cm dbh (diameter at breast height) for foraging (Mellen et al., 1992; Renken and Wiggers, 1993; Savignac et al., 2000). Nest and roost trees have been described as large diameter (>50 cm dbh) dead or live trees with decay in the Coast Range of western Oregon (Mellen et al., 1992), northeastern Oregon (Bull, 1987), south central British Columbia (Harestad and Keisker, 1989), Pacific Coast in Washington (Aubry and Raley, 2002b), southeastern Vancouver Island in British Columbia (Hartwig et al., 2004), and Alberta (Bonar, 2000).

Management guidelines developed as a result of the National Forest Management Act of 1976 (USDA, 1978) recommend retention of specified densities of snags across the landscape

* Corresponding author. Tel.: +1 541 962 6547; fax: +1 541 962 6504.
E-mail address: ebull@fs.fed.us (E.L. Bull).

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and maintenance of 121-ha patches of older forest for nesting pairs of pileated woodpeckers in dry coniferous forests in the Pacific Northwest Region on National Forest land. These recommendations were based on limited research, primarily conducted in the eastern United States in deciduous forests; home ranges of 53–160 ha have been reported in oak-hickory forests in Missouri (Renken and Wiggers, 1989). Subsequent research suggested that larger home ranges (257–1056 ha: Mellen et al., 1992; 407 ha: Bull and Holthausen, 1993) are more typical of pileated woodpeckers in conifer forests of the Pacific Northwest. As a result management recommendations and habitat suitability models have been developed for pileated woodpeckers based on research conducted from 1973 through 1990 in forested stands in the dry interior of northeastern Oregon (Bull et al., 1992b; Bull and Holthausen, 1993).

The effects of natural disturbance events such as insect activity, disease, wind, and fire have not been described for most species including the pileated woodpecker. These disturbances are the primary mechanisms that insure a continuum of snags, downed dead wood, and live trees with decay over time which pileated woodpeckers depend on for nesting, roosting, and foraging. For example, in the Blue Mountains of northeastern Oregon large-diameter ponderosa pines (*Pinus ponderosa*) killed by mountain pine beetle (*Dendroctonus ponderosae*) in the 1970s were later used as nest trees by pileated woodpeckers (Bull, 1987; Bull and Holthausen, 1993). A decade-long epidemic of the western spruce budworm (*Choristoneura occidentalis*) in the 1980s followed by Douglas-fir beetle (*Dendroctonus pseudotsugae*) outbreaks in the 1990s caused severe, wide-spread tree mortality in stands with grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) (Gast et al., 1991; Wickman, 1992). As a result, the forests described in the earlier studies on pileated woodpeckers have changed considerably from large continuous areas of mature and old forests with dense canopy cover (>70%; Bull and Holthausen, 1993) to relatively open canopies (<30% closure) and an increasing number of snags and logs.

Potential effects of extensive tree mortality and landscape change on the density of nesting pileated woodpecker pairs and reproductive success are unknown. The amount of canopy closure could influence a species vulnerability to avian predation. In Alberta, the density of cavity trees and foraging substrates was inversely related to territory size (Bonar, 2001). Previous research has demonstrated that increases in standing dead and downed wood are likely to positively impact prey availability (Bull et al., 1992a; Torgersen and Bull, 1995) and the number of potential nest and roost trees. To determine what habitat features influence reproduction, we present data comparing the density of nesting pairs and traditional home ranges of pileated woodpeckers in two study areas over a 30-year period, and in five additional study areas over 15 years after extensive insect-caused tree mortality and timber harvest in the 1990s.

2. Methods

2.1. Study areas

The density of pileated woodpecker nesting pairs was determined on the Starkey Experimental Forest and Range (hereafter referred to as Starkey) during 1973–83 (period 1) (Bull, 1987). Subsequently in 1989–90 (period 2) and 2003–05 (period 3), the density of pileated woodpecker nesting pairs was reexamined in two study areas (Bear and Syrup) within and comprising 27% of Starkey and determined in five additional study areas (Spring, McIntyre, Pelican, Balm, Ukiah); all seven study areas are within the Blue Mountains of northeastern Oregon (Table 1). Bear and Syrup are located 35 km southwest and 35 km west-southwest of La Grande, respectively. Spring is 16 km west of La Grande. McIntrye and Pelican are 26 km west and 16 km northwest of La Grande, respectively. Balm is 38 km southeast of Union, and Ukiah is 17 km west of the town of

Table 1
Study areas and habitat characteristics measured in pileated woodpecker studies during three time periods in northeastern Oregon

Variable	Time period		
	1 (1973–1983)	2 (1989–1990)	3 (2003–2005)
Study areas	Starkey*	Bear, Syrup, Spring, McIntrye, Pelican, Ukiah, Balm	Bear, Syrup, Spring, McIntrye, Pelican, Ukiah, Balm
Forest type	Ponderosa pine, Douglas-fir, grand fir (Burr, 1960)	Ponderosa pine, Douglas-fir, grand fir (Johnson and Hall, 1990)	Ponderosa pine, Douglas-fir, grand fir (Johnson and Hall, 1990)
Structural stage	Mature (Bull, 1980)	Young, mature, old growth (Bull and Holthausen, 1993)	Young, mature, old growth (Bull and Holthausen, 1993)
Harvest activity	Unharvested (Bull, 1980)	Unharvested, partial cuts, regeneration cuts (Wellner, 1978; Bull and Holthausen, 1993)	Unharvested, partial cuts, regeneration cuts, fuel reductions (Bull and Holthausen, 1993; Bull et al., 2005)
Canopy closure	0–10%, 11–59%, ≥60%	0–10%, 11–59%, ≥60% (Bull and Holthausen, 1993)	0–10%, 11–59%, ≥60% (Bull and Holthausen, 1993)
Density of snags <51 cm dbh	367 plots along transects (Bull et al., 1986)	360 plots (Bull et al., 1990b; Bull and Holthausen, 1993)	367 plots
Density of snags ≥51 cm dbh	367 plots along transects (Bull et al., 1986)	Complete count (Bull et al., 1990b)	367 plots
Log density	% log cover (Bull et al., 1986)	240 plots (Torgersen and Bull, 1995)	367 plots

* Bear and Syrup make up 27% of Starkey.

Ukiah. The seven study areas are in Union, Umatilla, and Baker counties on the Wallowa-Whitman and Umatilla National Forests. All study areas are 1454–1587 ha in size and between 1080 and 1800 m in elevation. Study areas contain a mosaic of mixed-coniferous stands composed of ponderosa pine, Douglas-fir, western larch (*Larix occidentalis*), grand fir, and lodgepole pine (*Pinus contorta*) interspersed with scattered grasslands.

2.2. Vegetation characteristics

Methods used to characterize the vegetation for the three time periods varied (Table 1), and the data are not entirely comparable as the earlier studies revealed additional variables that were important components of the habitat. During periods 1 and 2, aerial photographs (Avery, 1978) and field exams were used to delineate stand boundaries based on differences in vegetation type, tree size class, and amount of canopy cover. Following stand delineation, field examinations were conducted on each stand to collect information on plant series, structural stage, canopy cover, harvest history, and snag and log density (for details see Bull, 1987; Bull and Holthausen, 1993). In period 3, we used the vegetation data developed by the Wallowa-Whitman National Forest (Hemstrom et al., 2007). Stand boundaries and attributes were identified on 1:24,000 aerial photographs using National Forest Service photo interpretation and/or field stand examination standards.

In 1989–90 and 2003–05, harvest history was classified as unharvested, partial removals, regeneration cuts, and fuel reduction treatments. Unharvested stands included those that had never had any logging activity or that had been high-graded 20–50 years previously with only the valuable large-diameter seral tree species harvested (also called economic selective harvest; Wellner, 1978). Partial cuts included salvage cuts, sanitation cuts, commercial thinning, and selection cuts. Regeneration cuts included clearcuts, shelterwood removal cuts, overstory removal cuts, seed tree cuts with reserved trees, and shelterwood seed cuts. Fuel reduction treatments occurred primarily in Bear between 2001 and 2003 and removed ladder fuels, some green and dead trees 10–51 cm dbh, and downed material with the objective of retaining 18.4 m^2/ha basal area in live trees.

In period 1, snags and percent of log cover were characterized in plots on Starkey (Bull et al., 1986). In period 2, snags and logs were characterized in plots or using complete counts in all seven study areas (Table 1). In period 3, the number of snags and logs were determined in 50–60, 0.4-ha circular plots in each study area. We used a systematic placement of plots within a 500-m grid and UTM coordinates. Tree species, decay class, and size class (15–24, 25–37, 38–50, and $\geq$51 cm dbh) were recorded for all snags and logs.

2.3. Density of nesting pairs, reproductive success, and home ranges

Similar methods were used in all time periods to determine the density of nesting pileated woodpecker pairs and to locate nests (Bull et al., 1990a). Each study area was systematically searched for nesting pileated woodpeckers between 1 April and 15 May using call surveys along transects and by searching all stands within each study area that had trees large enough to contain a nest cavity ($\geq$51 cm dbh). Potential nests were observed to verify that they contained an incubating adult in May or nestlings in June. Nest trees were tagged and UTM coordinates were recorded. Northern goshawks (*Accipiter gentilis*) and Cooper's hawks (*A. cooperii*) detected during call surveys or nest searches were recorded in the 2003–05 surveys.

Reproductive success in periods 1 and 2 was determined by climbing nest trees to band or radio-tag young about a week prior to the young fledging. To determine reproductive success in period 3, fiberscope equipment was used at 2–3-week intervals when nest cavities were within 15 m of the ground, or nests were observed for at least 1 h when cavities were >15 m above the ground (Richardson et al., 1999; Nielsen-Pincus, 2005). Reproductive success was determined on Starkey in periods 1 and 3 and in the seven study areas in periods 2 and 3. Reproductive success could not be determined at all nests due to limited access.

In period 1, "nesting areas" were identified as the area where nest trees of a specific pair of pileateds (usually color-banded birds) were located between 1973 and 1983, although all nests were not found in all years (Bull, 1987). In period 2, home ranges of pileated woodpeckers were delineated from locations of radio-tagged birds. Birds were not radio-tagged in period 3; thus home ranges were defined as an ellipse 407 ha in size for each pair based on the average size and configuration of home ranges calculated for radio-tagged pairs in 1989–90 (Bull and Holthausen, 1993). The elliptical home ranges were positioned to encompass the nests, nest starts, drumming trees, and calling locations of each pair and minimize overlap between adjacent pairs in 2003–05. The amount of habitat in each forest type, structural stage, logging activity, canopy closure class, and non-forest was determined in each 407-ha area for each pair. "Traditional home ranges" were defined as the area used by multiple generations of pairs in a particular area. Nesting areas or traditional home ranges were identified on Starkey in periods 1 and 3 and in seven study areas in periods 2 and 3.

2.4. Analysis

Stepwise linear regression (Zar, 1999) was used to determine if habitat conditions (forest type, structural stage, canopy closure, logging activity in the last 15 and 30 years, snag density, and log density) explained the density of nesting pairs in the study areas in period 3. *T*-tests were used to test the effect of habitat on reproductive success with two different samples of pileated woodpeckers. We ran the first test using only those pairs for which success or failure was known for 2–3 years ($n = 11$). We ran a second test using all pairs for which success or failure was know for 1 or more years ($n = 26$).

3. Results

3.1. Vegetation characteristics

All stands within the seven study areas contained >90% live trees prior to and during the 1989–90 study. Stand characteristics

Table 2
Percent of seven study areas classified by structural stage, logging activity, and canopy closure in 1989 and 2003 in northeastern Oregon

Variable	Study area													
	Bear		Syrup		Balm		McIntyre		Ukiah		Pelican		Spring	
	1989	2003	1989	2003	1989	2003	1989	2003	1989	2003	1989	2003	1989	2003
Structural stage (%)														
Young	3	28	1	53	2	17	24	47	11	13	4	21	11	20
Mature	66	37	59	20	83	60	60	32	77	59	72	49	76	45
Old growth	17	10	27	0	12	13	10	6	7	21	11	3	3	11
Grassland	14	25	13	27	3	9	6	13	5	7	13	27	11	24
Logging activity (%)														
None/high-grade	78	49	86	37	31	72	19	62	6	93	20	61	5	73
Partial	2	7	<1	11	66	7	50	18	83	0	63	6	72	3
Regeneration	6	0	2	25	0	12	25	6	10	0	4	6	12	0
Fuel reductions		19		0		0		0		0		0		0
Canopy closure														
0–10%	5	28	<1	34	2	13	32	46	27	6	7	19	11	18
11–59%	36	47	34	38	52	43	29	34	54	68	57	47	65	53
≥60%	45	0	53	1	43	44	33	6	14	20	23	7	13	5

Harvest activity in 2003 was the percentage of each study area that had been harvested since 1990.

representing forest conditions in periods 2 and 3 are listed in Table 2. The spruce budworm and subsequent Douglas-fir bark beetle outbreaks resulted in extensive mortality of grand fir and Douglas-fir and a loss of canopy closure in the late 1980s and 1990s in all the study areas except Balm and Ukiah (Tables 2 and 3). Generally, the density of snags and logs increased after 1990 in the study areas with extensive mortality and without harvesting (Bear and Spring) (Table 3). Areas with extensive regeneration harvests (Syrup and McIntrye) resulted in a loss of both logs and large-diameter snags (Bull et al., 2005); mean density of logs across all seven study areas in 1989 was 219 ha^{-1} (Table 3).

3.2. Density of nesting pairs

Density of nesting pairs in period 3 (Table 4) was explained by three habitat variables in a step-wise linear regression ($r_a^2 = 0.93$) with a significant positive relationship with the amount of area in the late structural stage ($t = 4.28$, $P = 0.02$) and a significant negative relationship with the amount of area dominated by ponderosa pine ($t = -6.61$, $P < 0.01$) and the amount of area with regeneration harvests since 1970 ($t = -6.87$, $P < 0.01$). In six of the seven study areas (all except Syrup), the density of nesting pairs of pileated woodpeckers remained the same or increased or decreased by only 1 pair between periods 2 and 3, if additional pairs using the areas (although the nests were outside the area boundaries) are considered (Table 4). The density of nesting pairs in Bear remained the same in periods 1 and 2. For these six study areas, there was less harvest activity in the period from 1990 to 2003 than there had been in the decades preceding 1990. However, canopy closure declined in 5 of the 7 areas owing to tree mortality (Tables 2 and 3). There were few regeneration harvests and the total amount of mature and old forests decreased by less than 25% in the six study areas with consistent pileated woodpecker densities (Table 2). Even though some of the older stands consisted primarily of snags and were no longer classified as old growth, they continued to function as old growth habitat for woodpeckers because of the nesting, roosting, and foraging habitat provided.

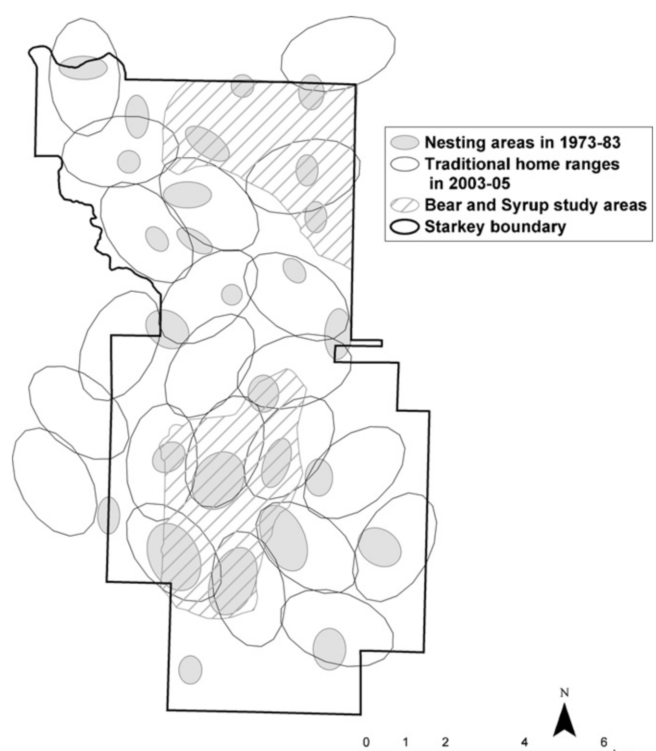

Fig. 1. Location of pileated woodpecker nesting areas in 1973–1983 and traditional home ranges used in 2003–2005 on the Starkey Experimental Forest and Range in northeastern Oregon. Traditional home ranges were based on the location of active nests in 1973–1983, 1989–1990, and 2003–2005, although all nests were not located in all years. Bear and Syrup study areas are shown in hatched areas.

Table 3
Mean density (S.E.) of snags and logs per ha in seven study areas in northeastern Oregon in 1989 and 2003

Variable	All areas	Study Area													
	1989	Bear		Syrup		Balm		McIntyre		Ukiah		Pelican		Spring	
		1989	2003	1989	2003	1989	2003	1989	2003	1989	2003	1989	2003	1989	2003
Snags dbh															
15–24 cm	‖	‖	26.9 (4.5)	‖	1.6 (0.3)	‖	6.1 (0.8)	‖	4.1 (0.6)	‖	2.6 (0.4)	‖	4.3 (0.7)	‖	6.5 (1.1)
25–50 cm	‖	6.8	29.0 (5.8)	8.7	3.0 (0.7)	4.3	5.6 (1.1)	6.2	6.1 (1.5)	6.6	2.1 (0.5)	9.0	4.8 (1.3)	3.1	4.0 (0.9)
≥51 cm	‖	2.7	5.6 (1.1)	1.8	0.1 (0.1)	0.4	0.4(0.2)	1.4	0.4 (0.1)	0.9	0.2 (0.1)	1.3	0.4 (0.2)	0.2	0.4 (0.2)
Logs															
15–24 cm	101	‖	172 (18.7)	‖	44 (4.7)	‖	54 (6.29)	‖	71 (5.8)	‖	52 (5.7)	‖	90 (8.4)	‖	45 (8.2)
25–37 cm	72	‖	71 (10.2)	‖	33 (3.6)	‖	25 (3.4)	‖	37 (4.7)	‖	37 (4.4)	‖	67 (6.7)	‖	29 (4.1)
38–50 cm	27	‖	17 (2.8)	‖	9 (1.8)	‖	10 (2.2)	‖	21 (0.2)	‖	15 (2.8)	‖	27 (4.6)	‖	12 (2.5)
≥51 cm	18	‖	11 (2.2)	‖	2 (0.8)	‖	2 (1.1)	‖	4 (1.8)	‖	4 (1.2)	‖	7 (1.6)	‖	2 (0.8)
Total logs	219*	‖	271	‖	88	‖	91	‖	133	‖	108	‖	191	‖	88

* Log density calculated in seven of the study areas in random plots and in plots used by radio-tagged pileated woodpeckers for foraging (Torgersen and Bull, 1995; Bull et al., 1997).

Table 4
Number of pileated woodpecker pairs nesting in two study areas during three time periods and in five study areas during two time periods in northeastern Oregon

Study area	Number of nesting pairs			
	Size of area (ha)	1973–1983	1989–1990	2003–2005
Bear	1624	7	7	6
Syrup	1454	5	5	1
Balm	1534		3 *	4
McIntyre	1460		3	1*
Ukiah	1585		3	4
Pelican	1656		2*	3
Spring	1616		1	0*
Total			24	17

* An additional pair used the study area but nested outside the study area boundary.

The largest decline in nesting density occurred in Syrup where only one pair nested consistently within the study area in period 3 compared to five pairs during periods 1 and 2 (Fig. 1). The most substantial impact to Syrup occurred in 1991 when 51% of the grand fir stands were logged with regeneration cuts; 14% of the forest area had partial cuts as well. In 2003, only 3% of the forested area occurred in mature or old-growth stands of grand fir, in contrast to 50% of the study area being grand fir in 1990 (primarily in old-growth and mature stands); stands of old growth and grand fir were favored by pileated woodpeckers in period 2 (Bull and Holthausen, 1993). The spruce budworm epidemic killed much of the remaining grand fir in this study area, but most of the fir trees had already been removed by harvesting. The harvesting and defoliating insect infestation resulted in an increase in openings and young stands, a decrease in stands with grand fir trees, an elimination of old growth and of stands with ≥60% canopy closure, and a decrease in snags and logs (Tables 2 and 3). The regeneration harvest of many mature or older stands greatly reduced the amount of suitable foraging, roosting, and nesting habitat for pileated woodpeckers.

The density of pileated woodpeckers had been monitored for over 30 years in both Bear and Syrup. In Bear, the density of nesting pairs remained the same in study periods 1 and 2 and decreased by one pair in period 3. The density of snags was similar with 50 ha^{-1} of which about 5 snags were ≥51 cm dbh (Bull et al., 1986) in period 1 and more than 60 ha^{-1} of which 5.6 snags were ≥51 cm dbh in period 3 (Table 3).

During call surveys and nest searches over 3 years in period 3 (total of 100–150 h per area), northern goshawks and Cooper's hawks were not detected in Ukiah and McIntyre and were detected once in Bear and Spring, twice in Balm, and three times in Syrup and Pelican.

3.3. Reproductive success

On all of Starkey, 83% of 81 nesting pairs fledged young between 1973 and 1983 (period 1; Bull and Meslow, 1988). In period 2, 75% of 12 nesting pairs fledged young in Bear and Syrup (Bull and Holthausen, 1993). In period 3 in all seven

Table 5
The average percentage of the forested portion of 407-ha home ranges for pileated woodpecker pairs by forest type, structural stage, logging activity, and canopy closure class

Habitat characteristic	Successful reproduction	Unsuccessful reproduction
Number of pairs	8	3
Forest type		
Ponderosa pine	15%	15%
Douglas-fir	40%	53%
Grand fir	45%	30%
Other forest types	0%	2%
Structural stage		
Young	38%	27%
Mature	45%	62%
Old growth	16%	11%
Logging activity		
No harvest	85%*	62*
Harvested	15%*	38*
Canopy closure		
0–10%	25%	23%
11–59%	72%	77%
≥60%	3%	0%

Eight pairs always fledged young and three pairs never fledged young on Starkey from 2003–05.
* Differed significantly between successful and unsuccessful pairs.

study areas plus all of Starkey, 72% of 53 nesting pairs fledged young. Habitat conditions within projected home ranges on Starkey (including Bear and Syrup) appeared to influence nest success in period 3. Eight pairs on Starkey successfully fledged young in 2 or 3 consecutive years and were not known to fail during the course of period 3. Three pairs failed to reproduce in 2 or 3 consecutive years and were not known to successfully fledge young. The amount of unharvested area was significantly greater ($t = -2.28$, $P = 0.05$) and the amount of area that was harvested was significantly less (any type of harvest activity; $t = 3.86$, $P < 0.01$) in home ranges occupied by pairs that successfully raised young compared to pairs that failed to raise young (Table 5). One of the most prevalent harvest activities on Starkey in 2001–03 included fuel reductions which resulted in a decrease in snags, logs, and foraging material for pileated woodpeckers (Bull et al., 2005). Forest type, structural stage, and canopy closure class did not differ significantly between these eight successful and three unsuccessful pairs.

After incorporating pairs in other study areas and pairs for which we had only 1 year of data on nest success in period 3 (an additional 12 pairs that had been successful and three pairs that had been unsuccessful), the amount of area in forests with ≥60% canopy closure differed significantly ($t = 2.43$, $P = 0.02$) between successful (mean = 26 ha, S.E. = 7.1) and unsuccessful pairs (mean = 6 ha, S.E. = 4.4).

3.4. Traditional home ranges

Pileated woodpeckers nesting on Starkey used the same general areas for 30 years and as many as 2–4 generations. Of the 19 nesting pairs located within the boundaries of Starkey (including the Bear and Syrup study areas) during period 3, 18 nests were located within the same nesting area as in period 1 (Bull, 1987) (Fig. 1). Although Syrup now only supported one of the five pairs it previously supported, that pair nested in a home range previously used in periods 1 and 2. It is highly unlikely the same individual birds were present 15 and 30 years later.

In period 3 in the other five study areas, pileated woodpecker pairs nested in 9 of the 12 home range areas that were used in period 2. Three home ranges used in period 2 did not have nesting pairs in period 3; however, an additional three pairs nested on the edge of three study areas in period 3. In Ukiah, the same three home ranges were used by pileated woodpeckers in periods 2 and 3, plus an additional pair nested in the southeast corner of the study area. The pair that nested in McIntyre in period 3, nested about 500 m from the nest tree used in 1990. In period 3 in Pelican, two pairs nested within 500 and 800 m of the nest sites used in 1990, and an additional pair nested in the northeast corner of the study area. In period 3 in Balm, three pairs nested in the same home ranges used in 1990, and a fourth pair nested within the home range of a radio-tagged bird that nested outside the study area in 1990. No nesting pairs were located in Spring in period 3 (Table 4).

In period 3, nesting pairs no longer occupied traditional home ranges that had been impacted by extensive regeneration harvests since 1991. Four traditional home ranges in Syrup and two in McIntyre were unoccupied in period 3. In McIntyre, 21% of the home range used by one radio-tagged pair in 1990 had been harvested with regeneration cuts which removed many of the roost trees used by the pair in 1990; the second pair no longer nested in an area with 17% in regeneration cuts occurring between periods 2 and 3. One pair remained in a home range with extensive tree mortality but little harvesting.

4. Discussion

The recommendations for maintaining pileated woodpecker habitats in the interior Pacific Northwest written in 1993 suggested that home range habitat should be primarily (75%) in grand fir forest types of mature and older trees with at least 50% of the area in forests with dense canopies (>50% canopy closure) and limited harvest activities (Bull and Holthausen, 1993). These recommendations were based on research conducted in green forests before widespread disturbances (insect outbreaks) occurred across landscapes in northeastern Oregon. While most studies represent a temporal snapshot and cover a short duration, this study is unusual in that it encompasses a 15- and 30-year span and covers 2–4 generations of this long-lived species; estimates suggest a life span of at least 9 years (Bull and Jackson, 1995). Each of the three time periods of research in this study represents a relatively narrow window of forest succession and may not reflect forest condition changes brought about by large-scale disturbance and succession. In revisiting these study areas in some cases after 30 years, we found that the high tree mortality and loss of canopy closure (Tables 2 and 3) in stands of grand fir and Douglas-fir did not appear to be detrimental to pileated woodpeckers provided that large dead or live trees and logs were abundant (Table 3) and that stands were not subject to extensive harvest (i.e., concerted regeneration or fuel reduction harvests). In Bear, the high density of logs (271 ha^{-1}) and snags (>60 ha^{-1}) in period 3, the lack of regeneration harvests, and the older stands likely provided adequate habitat to support a high density of pileated woodpeckers. Whereas, extensive regeneration harvesting resulted in lower densities of pileated woodpeckers in the Syrup study area.

Decline of pileated woodpeckers could have a negative cascading effect on those species using pileated woodpecker's cavities and result in a subsequent decline in forest biodiversity. More than 20 species have been observed using pileated woodpecker cavities within these study areas. Pileated woodpeckers are considered a keystone species in western Oregon because 24 other wildlife species use their nest or foraging cavities including five species of waterfowl, five owls, two bats, four squirrels or woodrats, ringtails (*Bassariscus astutus*), American martens (*Martes americana*), fishers (*M. pennanti*), and four other cavity-nesting bird species (Aubry and Raley, 2002a). In Alberta, more than 18 other species used pileated woodpecker's cavities, some of which required a cavity of this size for nesting, including goldeneyes (*Bucephala* spp.) and buffleheads (*B. albeola*) (Bonar, 2000).

The habitat variables that best explained the density of nesting pairs in period 3 differed somewhat from those variables identified in period 2 (Bull and Holthausen, 1993). Both time periods identified a positive relationship with the amount of area in late structural stage, and a negative relationship with the amount of area with regeneration harvests or a positive relationship with the amount of area with no harvesting. Period 3 differed from period 2 in identifying a negative relationship between pileated nesting density and the amount of area in ponderosa pine stands and no significant relationship with density of snags $\geq$51 cm dbh or canopy closure. This change since period 2 resulted from the lack of a nesting pair in the Spring area in period 3 which is dominated by stands of ponderosa pine. Although pileated woodpeckers favor ponderosa pine trees for nesting in northeastern Oregon, nests in ponderosa pine trees most commonly occur in stands of mixed conifer (Bull et al., 1986). Stands of pure ponderosa pine in northeastern Oregon typically lack the abundance of snags and downed wood necessary for foraging habitat. The lack of a relationship between pileated density and canopy closure may be because there were few stands that contained $\geq$60% canopy closure in five of the study areas in period 3. The lack of relationship between large-diameter snags and pileated density suggests that nest trees may not be limiting in these study areas.

One anticipated effect of forest disturbance on pileated woodpeckers was an increase in avian predation owing to a lack of protective cover with a subsequent decrease in pileated density. Accipiters were responsible for more than a third of the predation detected in pileated woodpeckers in period 2 (Bull, 2001). By period 3, the stands that were used for nesting by goshawks in the 1970s and 1980s no longer contained forests with live, large-diameter trees and dense canopy closure which has been described as suitable nesting habitat for goshawks (Squires and Reynolds, 1997). Although the mature and old-growth stands with extensive mortality provided nest and roost trees and foraging substrate for pileated woodpeckers (Bull et al., 2005; Nielsen-Pincus, 2005), few accipiters (0–2) were detected during surveys in the study areas with extensive tree mortality, and density of pileated pairs was not substantially less than in previous periods.

Insect outbreaks are natural disturbances that occur at intervals over time in dry coniferous forests of the western United States. Disturbance events are the primary mechanism that insures a continuum of snags or live trees with decay over time which these woodpeckers depend on for nesting, roosting, and foraging. In northeastern Oregon, a mountain pine beetle epidemic in the 1970s killed large-diameter ponderosa pines that were used by pileated woodpeckers for foraging in the 1970s and for nesting in the 1970s and 1980s (Bull, 1987). The grand fir and Douglas-fir trees used for nesting in 2003–05 (Nielsen-Pincus, 2005) likely were killed by the spruce budworm or Douglas-fir bark beetle outbreaks during the 1980s and early 1990s. Additionally, many of these resulting predominantly dead stands with large snags and logs were then used extensively for foraging by pileated woodpeckers (Bull et al., 2005). Short (1982) reported that some woodpeckers, notably the "three-toed" woodpeckers (*Picoides tricactylus*), may concentrate their numbers owing to an abundance of prey when insect populations reach epidemic proportions as occurs after stand-replacement fire.

Although the spruce budworm and Douglas-fir bark beetle outbreaks that occurred in the study areas by early 1990s decreased forest canopy closure, abundance of live grand fir forest types, and the density of large, live trees during the ensuing years, we did not observe any decreases in pileated woodpecker densities except in areas where extensive regeneration harvesting occurred. Different kinds of disturbances have variable effects on cavity-nesting birds, and each species differs in diet and habitat preferences. In British Columbia, thinning in dry Douglas-fir and ponderosa pine forests resulted in a decline in snag densities, cavity-nesting bird densities, and species richness of cavity nesters (Machmer, 2002). In stand-replacement fires in ponderosa pine stands in Idaho, nesting success was highest in unlogged controls for hairy woodpeckers (*P. villosus*) and mountain bluebirds (*Sialia currucoides*), highest in a standard salvage for Lewis' woodpeckers (*Melanerpes lewis*), and highest in a modified salvage for northern flicker (*Colaptes auratus*) and western bluebird (*Sialia mexicana*) (Saab and Dudley, 1998). Snag and log loss has been documented in prescribed burns in southwestern ponderosa pine forests (reviewed in Finch et al., 1997; Randall-Parker and Miller, 2002). Stands with fuel reduction treatments at Starkey had significantly fewer logs, fewer logs with ants, and less pileated woodpecker foraging in the burned treatments compared to the controls and mechanical fuel reductions (Bull et al., 2005); nest trees were also consumed by prescribed fire in several units. The long-term effects of fuel reductions on pileated woodpeckers are unknown, although with less log cover and fewer trees and snags to replace logs when they deteriorate, it is likely that foraging strata will not be replaced for decades or longer.

In northeastern Oregon, pileated woodpeckers foraged on carpenter ants (Camponotus spp.; 68%), thatching ants (Formica spp.) and other ants (29%), beetles (Coleoptera; 0.4%), and other invertebrates (2%) (Bull et al., 1992a). The association of carpenter ants with stumps and logs as temporary nest sites and living trees as permanent nest sites in Ontario (Sanders, 1970) somewhat parallels the observations of pileateds foraging in logs (38%), snags (38%), live trees (18%), and stumps (6%) in northeastern Oregon (Bull and Holthausen, 1993). In contrast, pileated woodpeckers fed almost exclusively on standing structures and selected tall, large-diameter snags in early to moderate decay in coastal forests in Washington; logs in coastal forests are apparently too cool and wet to support abundant numbers of carpenter ants, their primary prey (Raley and Aubry, 2006). In general, foraging sites on Vancouver Island, British Columbia, contained more coarse woody debris, a greater basal area of snags and defective trees and more western redcedar (*Thuja plicata*) than sites without foraging activity (Hartwig et al., 2006). In New Brunswick, foraging sites contained larger and more decayed trees than were available at random (Flemming et al., 1999).

4.1. Reproductive success

Information on nest success is critical in determining how effective the habitat is in meeting the needs of a species. If recruitment is low and mortality is high, sink populations are created (Van Horne, 1983). At Starkey, the pileated woodpeckers occupying home ranges with the least amount of harvested forest were the most successful at fledging young consistently. A lack of harvesting insured that an abundant number of snags and logs occurred in the unharvested grand fir stands as a result of spruce budworm outbreaks. In contrast, pairs occupying home ranges with extensive regeneration cuts or fuel reductions consistently failed to fledge young at Starkey.

4.2. Traditional home ranges

Pairs mate for life, defend territories year-round, and a surviving mate stays within a territory (Bull and Jackson, 1995). Pileated woodpeckers did not leave their home range even when they lost a mate; the single birds expanded the home range boundaries and increased the amount of overlap with neighboring pairs in search of a mate at Starkey in 1989–90 (Bull and Holthausen, 1993). Pairs were unlikely to leave their home range even when the habitat within the home range was altered in these study areas, as suitable unoccupied habitat was not available. If habitat becomes unsuitable, resident birds may continue to occupy the home range until they die, but it appears these habitats are not reoccupied later as occurred in Syrup. Individuals commonly acquire a territory by replacing a pair member that has died; floaters (nonbreeding birds) are sometimes tolerated within a territory and may be young birds that dispersed in the fall (Bull and Jackson, 1995).

The locations of pairs and nests were remarkably consistent between periods 2 and 3 in all areas without extensive regeneration harvests. On Starkey, nests were in some of the same stands in periods 1, 2 and 3 (Fig. 1). These observations suggest that nesting areas are fairly stationary over time if the habitat has not been altered, and it is likely that the area may be occupied subsequently by offspring or other dispersing birds. This information provides managers with the ability to spatially prioritize areas with high probabilities of occupancy by pileated woodpeckers over time. Traditional home ranges or nesting areas may be delineated partially by landscape features. The close proximity of some nest trees over the years may be a function of large-diameter ponderosa pines typically being on ridges in these study areas, and the snags are continually created in the same stands of larger trees.

Fidelity of color-banded adult pileated woodpeckers (26 adults) from 1973 to1983 was high with no adult moving from one territory to another; nests in successive years from 1973–83 were 0–1.16 km apart (Bull, 1987) which is within the 2.2-km diameter of a circular 407-ha territory (Bull and Holthausen, 1993). Other year-round resident species of woodpeckers were also reported to have a high fidelity to the breeding site or home range (white-headed woodpecker (*Picoides albolarvatus*)- Garrett et al., 1996; black-backed woodpecker (*P. arcticus*)- Dixon and Saab, 2000; three-toed woodpecker- Leonard, 2001). Reuse of the same breeding site or home range, in contrast to more nomadic behavior, may be a behavioral adaptation for survival, although this concept warrants further study.

5. Conclusions

Pileated woodpeckers continued to occupy landscapes with extensive tree mortality from insect outbreaks 15 years after the initial outbreak. Nesting density was positively associated with the amount of area in late structural stages and negatively associated with the amount of area in regeneration harvests and in ponderosa pine forest types. Pileated woodpecker densities declined in areas with extensive harvesting, but increased or remained the same in areas with tree mortality but without extensive harvesting.

Overall nest success was similar among the three time periods, although the highest success occurred in 1973–83. The amount of unharvested stands and closed canopy stands in home ranges were positively correlated with nest success; unharvested stands had a high density of snags and logs on Starkey (Bull et al., 2005). The amount of area in harvested stands was negatively correlated with nest success.

Insect outbreaks are a natural disturbance event that is an integral part of maintaining nest, roost, and foraging habitat for pileated woodpeckers in northeastern Oregon. This species is able to adapt to using a variety of tree species and habitat conditions, although large trees still appear to be essential. Closed canopy forests were not essential for use by pileated woodpeckers, although nest success was higher in home ranges that had greater amounts of forested habitat with $\geq$60% canopy closure. Harvesting, particularly regeneration cuts, were detrimental to this species. With the National Fire Plan (USDA and USDI, 2001) and Healthy Forest Restoration Act (HFRA, 2003) and management emphasis on fuels management and forest restoration, large areas have or will be subject to fuel reduction activities. Prudent resource management for wildlife dependent on coarse woody debris (snags and downed wood), like pileated woodpeckers, will consider the long-term effects of these activities (Pilliod et al., 2006).

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